

Borings and pseudoborings in Cincinnatian carbonate substrates of Ohio, Indiana, and Kentucky (Upper Ordovician)

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INTRODUCTION

The Upper Ordovician fossils and alternating mudstones and limestones of southwestern Ohio, southeastern Indiana, and northern Kentucky exhibit a variety of borings in hard substrates. Only three boring ichnogenera have been documented from the Cincinnatian: *Trypanites*, *Petroxestes*, and *Ropalonaria* (Hannibal, 1996). The research reported here indicates that Cincinnatian strata contain a greater variety of borings, especially in the Whitewater Formation of Indiana and the Grant Lake Formation of Ohio.

Boring allows organisms to exploit habitats within hard substrates (Warne, 1975); although macroborings are first seen in the Cambrian, borers do not significantly radiate until the Ordovician (Sepkoski, 1993; Bottjer and Droser, 1994).

Borings may preserve interactions between borers and living hosts as well as successions of organisms associated with the host. Past habits, lifestyles, and interactions of species are commonly difficult to study because little direct evidence is preserved in the fossil record; borings provide an opportunity to collect this type of ecological information.

Bioerosion rates, controlled primarily by borers, are considered low in the Paleozoic (Wilson and Palmer, 1992). Because Paleozoic borings are not well researched, this conclusion is not well supported.

The purpose of this study is to examine closely the types of borings that exist in Cincinnatian fossiliferous substrates, to determine any relationships between the host and the borer, and to calculate maximum bioerosion rates for the Cincinnatian region during this time.

LOCALITIES

In Kentucky, specimens were collected at the Maysville Bryozoan Reef Mounds (locality KY-MS-0006 of Davis et al., 1998) and at the AA highway (38°35'09"N, 83°42'07"W) sites (Grant Lake Formation; Bellevue Member of the McMillan Formation). In Indiana, specimens were collected at the Richmond (IN-WY-0001), Bon Well Hill (IN-FR-0001), and Garr Hill/Brookville North (IN-FR-0003) sites (Excello, Waynesville Shale, and Liberty Members of the Brookville Formation; lower Whitewater and Saluda Members of the Whitewater Formation).

PROCEDURE

After collection, bored specimens were examined in hand sample and acetate peels were made (see Wilson and Palmer, 1989). Microscopic examination of acetate peels yielded descriptions of borings, borer preferences, and hosts' reactions. Bryozoan specimens that appeared to have the greatest density of borings were used to calculate the maximum amount of bioerosion. Specimens were sliced into 50-mm increments and the total and bored areas of each slice were determined using *NIH Image* software. The approximate total and bored volumes were calculated using simple mathematical equations.

BORING ICHNOGENERA

Trypanites Mägdefrau (Fig. 1) is a cylindrical boring with a diameter ranging from 1 to 2 mm. The depth of the boring may vary, but its length is greater than its width. The boring is straight and typically vertical, but in some cases may be horizontal. *Trypanites* was probably made by polychaete annelid worms (Elias, 1980, 1986).

Petroxestes Wilson and Palmer (Fig. 1) is a large, elongate boring with rounded edges; it can be up to 30 mm long, 6 mm wide, and 20 mm deep. Boring mytilid clams probably produced *Petroxestes* (Wilson and Palmer, 1988).

Ropalonaria Ulrich (Fig. 2) is a shallow, bilaterally branching boring that commonly occurs in brachiopod shells. It was probably made by a boring ctenostome bryozoan (Pohowsky, 1978).

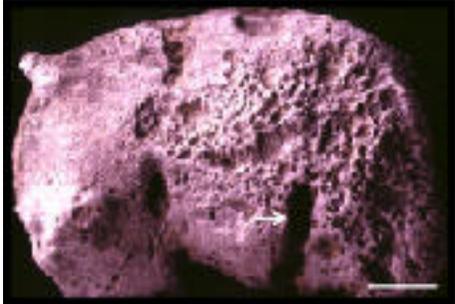


Figure 1. *Trypanites* (smaller borings in structure). Scale bar 1 cm.

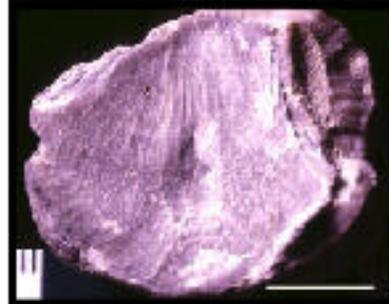


Figure 2. Brachiopod with *Ropalonaria* (narrow branching surface view) and *Petroxestes* (white arrow). Scale bar 1 cm.

Cincinnatian borings are created primarily by soft-bodied organisms that typically are not preserved. Because different borers can make excavations with similar morphologies, borers rarely can be associated with a boring if they are not preserved (Frey, 1975).

BORINGS IN BRACHIOPOD AND BIVALVE SHELLS



Figure 3. Exterior of brachiopod valve exhibiting lateral borings. Scale bar 1 cm.

Lateral borings on the exteriors of brachiopod valves are preserved as ditch-like excavations (Fig. 3). Because aragonite dissolved on the Ordovician seafloor, borings in aragonitic bivalve shells typically are preserved in two ways: as casts composed of cemented sediment and as ditch-like excavations through bryozoans that encrusted the bivalve shells. All three types of preservation suggest that borings are cylindrical and were cut at the interface between an encrusting bryozoan and a brachiopod or bivalve shell. Typical lateral borings are relatively straight in map view, but some may show gentle curving; these borings commonly show a slightly clavate (club-like) expansion at their termini. Ditch-like excavations in brachiopod shells are shallow, and, if assumed to be cylindrical, represent from 5% to 30% of the boring; lateral borings found in encrusting bryozoans are deeper than those found in brachiopod shells, typically representing more than 50% of a cylindrical boring. These data suggest that more of the boring is found in the encrusting bryozoan than in the underlying brachiopod shell; the same can be assumed for bivalve shells. Borings that are preserved as casts represent the entire cylindrical boring.

Most lateral borings seen in bryozoans and brachiopods are only part of the total boring; the true form of the boring is L-shaped, cutting vertically through an encrusting bryozoan and horizontally through both the bryozoan and the shell along the bryozoan-shell interface (Lazzuri et al., 1999). These L-shaped borings with clavate termini resemble the ichnogenus *Palaeosabella* rather than *Trypanites* (see Palmer et al., 1997); *Palaeosabella* has not previously been documented from the Ordovician.

The difference in substrate may be the reason for change in boring direction. Bryozoan skeletons are less dense (and possibly easier to bore) than brachiopod or bivalve shells because of their open zooecia. Similarly, it is possible that the borer preferred to excavate along the bryozoan-shell interface because this surface was weaker than either the bryozoan skeleton or the shell.

BORINGS IN BRYOZOAN SKELETONS

Borings that occur in Cincinnatian ramose and massive trepostome bryozoans tend to be simple in form: straight, curved, or ditch-like excavations. These morphologies technically fit the description of the ichnogenus *Trypanites* (Bromley, 1972); however, the variety that exists within each group (see below) suggests that perhaps *Trypanites* is circumscribed too broadly.

Straight borings. Straight borings do not curve more than 5°. They range in length from 0.5 to 15.0 mm and in width from 0.25 to 2.0 mm. Some straight borings cut through the entire zoarium; others are confined to zooecia, cutting only diaphragms.

Type 1: vertical or diagonal; rough edges; boring width uniform; unlined.

Type 2: vertical or diagonal; rough edges; boring width increases at terminus; unlined.

Type 3: vertical or diagonal; rough edges; boring width tapers at terminus; unlined (Fig. 4).

Type 4: vertical; rough edges; boring wide at top, tapering twice; unlined.

Type 5: vertical or diagonal; rough edges; boring width uniform; lined.

Type 6: vertical or diagonal; rough edges; boring width increases at terminus; lined.



Figure 4. Composite photomicrograph of a straight boring (Type 3). Scale bar 1 mm.

Curved borings. Curved borings are any excavations that curve more than 5°. Curving generally occurs at the boring's terminus. Curved borings range in length from 0.5 to 9.5 mm and in width from 0.25 to 1.5 mm. Curving typically occurs just above a line of rejuvenation in a bryozoan or above a change in substrate.

Type 1: vertical; rough edges; boring width uniform; unlined.

Type 2: vertical; rough edges; boring width increases at terminus; unlined (Fig. 5).
Type 3: vertical; rough edges; boring width uniform; lined.

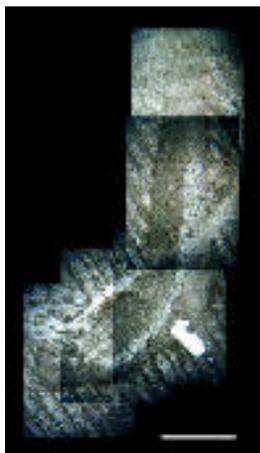


Figure 5. Composite photomicrograph of a curved boring (Type 2). Scale bar 1 mm.

Ditch-like borings. Ditch-like borings are shallow in depth, cutting up to 0.5 mm into a bryozoan.

Type 1: dish shaped; width and depth approximately equal; slightly raised edges; unlined.

BORER PREFERENCES IN BRYOZOAN SKELETONS

Borings occur in all parts of bryozoans, but some areas are more commonly excavated than others. In the specimens observed for this study, borings commonly occur in the following places: 1) the endozones of trepostome bryozoans, 2) above lines of rejuvenation, and 3) within zooecia, cutting only diaphragms.

Borers may prefer to cut the endozones of trepostome bryozoans because the exozone, with its tightly packed diaphragms, may be more difficult to bore through than the less dense endozone.

Many specimens with lines of rejuvenation show a high occurrence of borings curving just above the line, in the endozone; in some cases the boring continues at an angle parallel to the line of rejuvenation. Borers may find the less dense skeletal material in the endozone easier to bore than the material in the exozone; or, possibly the line of rejuvenation represents a weak area that is easier for the borer to excavate.

Borings may be excavated within zooecia, cutting only through diaphragms. Again, it seems that cutting through diaphragms would be easier for a borer than cutting through both diaphragms and walls, especially since walls are thicker than diaphragms (McKinney and Jackson, 1989). It is also possible that this method of cutting is desirable because the borer would be surrounded by smooth walls instead of the rough, jagged edges of cut walls.

BRYOZOAN REACTION TO BORING

Host reactions to borers are difficult to quantify because if there is no visible reaction, the host either was not living when bored or was living but not affected by the boring. Thus, the following descriptions only include observations from those specimens that show clear evidence of reactions by living hosts.

Borings that exist below lines of rejuvenation are covered by episodes of growth that occurred after boring. Borers may or may not have been alive at the time of new growth; however, the bryozoan was able to repair itself from past or current damage.

Areas of local rejuvenation also may occur. Localized regrowth of skeletal material shows that the bryozoan was still living when it was bored and that repair did not require the regrowth of the entire colony. Localized regrowth has been observed on modern damaged stenolaemates (McKinney and Jackson, 1989).

PSEUDOBORINGS

Pseudoborings appear as circular, raised areas on bryozoan skeletons. In most cases, cut walls are not associated with the raised areas, suggesting that they are cavities around which the bryozoan grew. In most cases, pseudoborings rest on top of a mature zone and are the only relief above this zone.

Pseudoborings may be generated in a number of different ways. A soft-bodied organism, or paraendolith, may have landed on a bryozoan and triggered a response. It may have competed with surrounding zooids for food. Because of this pressure, new zooids may have grown in a raised position around the paraendolith, making it difficult for it to obtain food. If the paraendolith secreted chemicals in order to compete, the new zooids could be replacing the ones lost in competition. This method seems plausible since most extant and extinct borers use/used chemical means to excavate substrates (Palmer and Plewes, 1993).

BIOEROSION

The total bored volume of Cincinnati trepostome bryozoan skeletons ranges from about 6.8% to 21.4%, with the majority falling around 10% (Table 1). Although many of the specimens contained large numbers of borings (some with over 250), most borings were so small that the resulting volume removed was low. These data are helpful in tracking bioerosion rates through the Phanerozoic.

Table 1. Bioerosion data for eight trepostome zoaria

Specimen	Total Volume Bored (mm ³)	Total Volume of Specimen (mm ³)	Percent of Specimen Bored
1	18155.8	267065.5	6.8
2	22252.1	296714.4	7.5
3	16798.9	179956.0	9.3
4	17090.1	181587.0	9.4
5	29988.4	281976.5	10.6
6	84260.4	757578.9	11.1
7	26648.6	219300.0	12.2
8	73719.6	344391.9	21.4

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